The Chromodoridinae Nudibranchs from the Pacific Coast of America. - Part I. Investigative Methods and Supra-Specific Taxonomy

BY

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(3 Text figures)

INTRODUCTION

CHROMODORID NUDIBRANCHS are a worldwide tropical group, noted for their distinctive and beautiful color patterns. The group has been studied extensively, with numerous papers in part dealing with members of the Chromodorididae. This contribution is the first in-depth treatment of all the known species of the Chromodoridinae from the Pacific coast of America. Previous studies of this group from American Pacific waters have been based on a very small number of dissected specimens or only a few species (e.g., MacFarland, 1966; Marcus & Marcus, 1967; Bertsch, 1970). Modern reviews of the Chromodorididae from other geographic provinces (Indo-Pacific: Rudman, 1973; Australia: Thompson, 1972; Hawaii: Kay & Young, 1969) are also based upon small numbers of dissected specimens of each species.

By obtaining specimens from several major museums, and making many collecting trips to Mexico and Panama, I have obtained a large quantity of specimens, which I dissected and examined critically. Visual and numerical data obtained from these dissections were used to revise systematically the genera and species of the American Pacific coast Chromodoridinae.

Principles governing the use of the radula in opisthobranch systematics have been proposed by Bertsch (1976 a). This study applies Bertsch's methods of examining opisthobranch radular variation (multiple meristic counts and measurements, ontogenetic patterns, and morphological studies using light microscopy and scanning electron microscopy) to a large group of phylogenetically related nudibranchs. Radular morphology and meristic qualities, and the external coloration are diagnostic characters for each of the 15 species of the Chromodoridinae from the Pacific coast of America.

The following abbreviations refer to the collections from which nudibranch specimens were obtained:

USNM - United States National Museum of Natural History (Smithsonian Institution), Washington, D. C.

CAS - California Academy of Sciences, San Francisco, California

LACM - Los Angeles County Museum of Natural History, Los Angeles, California

HB - Hans Bertsch

MATERIALS AND METHODS

Scanning Electron Microscopy

In the past few years, the scanning electron microscope has become a significant source of visual data for malacologists studying the ultrastructure, taxonomy, and functional morphology of various mollusks. It has been used to depict veligers (Robertson, 1971b), adult shells (e. g., Solem, 1970; Thomas & Bingham, 1972; Margolis & Carver, 1974), chiton girdle scales (Ferreira, 1974, 1976), body soft parts (Arcadi & Hodgkin, 1973; Murray & Lewis, 1974), spermatozoa (Maxwell, 1975), fossil eggs (Tompa, 1976), a fossil radula (Solem & Richardson, 1975), and radulae of living mollusks (e. g., Solem, 1972).

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Because of the SEM's clear resolution in the 300-10000 magnification range and its 3-dimensional imaging of biological samples, it is ideal for studying the total morphology of opisthobranch radulae, the details of individual teeth, and interrelationships between movable parts. Thompson & Hinton (1968) published the first scanning electron micrographs of opisthobranch radulae. Bertsch (1970) first used the SEM to illustrate the radula in a new species description of an opisthobranch. Since then, stereo pair micrographs have been published (Bertsch et al., 1973), other workers have begun using SEM to illustrate opisthobranch radulae (e.g., Mulliner & Sphon, 1974; Bouchet, 1975), and scanning electron micrographs have become an established method for presenting information about opisthobranch radulae.

The principles of operation of the SEM and its biological applications are extensively documented. An entry to this literature can be gained by consulting the papers by Hayes (1972, 1973) and EVERHART & HAYES (1972).

The recent increase of published scanning electron micrographs necessitates a few precautionary words about their interpretation. Certain artifacts (avoidable or not) are inherent in the preparation and viewing processes of SEM. Clark & Glagov (1976) have discussed 3 types of artifacts: accretion of extraneous materials, distortion of real cell and tissue surface details during processing, and distortion during viewing (including "charging," cf. Pawley, 1972).

There are 2 additional artifacts that can occur by uncritical examination of SEMs: the "2-headed cow" effect (T. L. Hayes, personal communication), and the "other side of the coin." The first artifact involves the interpretation of different planes that are visible in a micrograph. People can easily separate objects seen in the everyday macroscopic world as occurring at different depths in our field of vision (we know that the 2-headed cow is actually 2 cows standing together in opposite directions), but the same phenomenon in the microscope may pass unrecognized and be described as an ultrastructural unit. It is the advantage of the SEM - providing great depth of field with high resolution — which causes this possibility of planar reversibility. Analysis of overlapping and shading on the micrograph will often eliminate this problem, but sometimes it can be resolved only by stereopair or by rotating the specimen 90° so that the planes in question are aligned parallel, rather than perpendicular, to our field of vision.

The second artifact also stems from the imaging properties of the SEM. Image formation occurs by a time sequencing of points on the specimen surface with points on the cathode ray tube. This contrasts with the light and transmission electron microscopes' transparent technique

of point-to-point spatial correspondence between the specimen and its image. Because the SEM operates by temporal sequencing across a non-transparent object, the researcher does not know what is on the obverse side of the object being examined. The observer is looking at rather rather than through the specimen. Prevention of unduly assuming bilaterality requires tilting or rotating the specimen, reorienting the specimen on the mounting platform, or (if the details are large and the specimen thin enough) viewing the specimen with a light microscope.

Specimen Preparation

In this study, I dissected and examined over 270 radulae. By using such a large sample size, by comparing light and scanning electron microscopy, by taking stereo-pair micrographs, and by frequent tilting and rotation of puzzling specimens in the SEM chamber, descriptions of the radular teeth were carried through a rigorous checking to insure their accuracy and usefulness to other researchers.

Radular preparation involved dissecting the buccal mass, dissolving the tissues surrounding the radula with a cold bleach (sodium hypochlorite) solution (cf. Lindberg, 1977), and then allowing the radula to rinse in a 70% ethanol solution. For light microscopy, the cleaned radula was placed flat on a standard microscope slide, allowed to air dry, and then sealed under a cover slip with Permount mounting fluid.

Radulae that were to be examined with SEM were dissected and cleaned in the same way. After rinsing, each radula was mounted on a petrographic slide without a cover slip, air dried, and then covered with a thin layer of gold by vacuum evaporation to improve specimen conduction and reduce charging. The radular ribbon was bent or torn in places so that lateral views of the teeth could be obtained from the SEM. Any shrinkage or bending caused by the air drying did not significantly distort the rigid teeth shapes; moreover, it often allowed lateral and basal examination of the teeth. Specimens were viewed with a Japan Electron Optics Laboratory Co., Ltd., Scanning Type Electron Microscope Model JSM, at either 10 or 25 kV accelerating voltage. After examination with the SEM, each radula was covered with a cover slip and observed with a light microscope. The gold layer did not interfere with the transparency of the radula to visible light, but enhanced the resolution by acting as a surface stain.

Mounting the radula on the smaller-sized petrographic slide permits successive viewing of the specimen by SEM and light microscopy. The petrographic slide is small enough to fit on the specimen holder inside the SEM vacuum chamber, and is transparent to light. Similar tech-

niques for comparative imaging of the same specimen have been used previously by McDonald & Hayes (1969) and Barber (1972).

Numerical Analysis of Radular Variation

Statistical studies of dentition form an important corpus in the understanding of mammalian taxonomy and vertebrate community structure. Examining large numbers of mammal specimens, authors of new species and revisers have given particular attention to numbers of teeth, means of sizes, and other measurements and counts (the literature is extensive, and only a few citations are necessary; cf. Mooser & Dalquest, 1975, or Villa-R., 1966). Recent papers by Grant (1967), Roughgarden (1974), and Tamsitt (1967) have estimated trophic relationships of vertebrate communities by analysis of the comparative morphology of trophic structures (bird bills, lizard jaws, and bat jaws). Findley (1976) included measurements of feeding structures in his investigation of the phenetic structure of tropical and temperate bat communities.

By contrast, statistical treatment of molluscan teeth has been relied upon much less. Although knowledge of the radula has advanced considerably since Aristotle's brief descriptions of the cephalopod radula ("a minute organ of a fleshy nature, and this it uses as a tongue, for no other tongue does it possess" - Ross, 1952: 50) and that of the "spiral-shaped testaceans" ("Some of these creatures have a mouth and teeth, as the snail; teeth sharp, and small, and delicate" - Ross, op. cit.: 55), most treatments of the radula have emphasized just morphology, and not ontogenetic changes nor inter- and intraspecific size variation.

TROSCHEL'S works (1856-1863, 1866-1893) are a notable exception, since he gave the sizes of most of his illustrated radulae and even indicated that larger specimens can have correspondingly greater-sized teeth ("Die Breite der Mittelplatte des abgebildeten Exemplars ist 0.085 Millim.; an einem grösseren Exemplare messe ich 0.11 Millim." - vol. I: 111).

In recent years, a number of articles have appeared discussing mathematical variations in radular teeth. Of special note is a series of papers by Schilder & Schilder (1961 a, 1961 b, 1963) and Schilder, Schilder & Houston (1964), in which numerous cowrie radulae are examined by regression analyses and mean sizes to determine sexual dimorphism and correlations between shell and radular sizes. Robertson (1971 a), reviewing reports of sexually dimorphic radulae among the Muricidae and Buccinidae, discusses meristic and morphological sexual dimorphism and population differences in the radulae

of a phasianellid; he speculates on the possible evolutionary significance of the dimorphism and illustrates the male and female radulae with scanning electron micrographs. Bandel (1974) and Borkowski (1975) studied the variability of Caribbean Littorinidae radulae. Finally, Bloom (1976) correlated radular tooth curvature (amount of concavity of the inner [sic] margin of the tooth) with sponge prey items of dorid nudibranchs.

Variation in size and number of opisthobranch radular rows and teeth has been considered taxonomically important for over a century. The use of these characters has been primarily typological (in the sense of Dobzhansky, 1970: 126, and Mayr, 1970: 3-5), resulting in the descriptions of intraspecific variations as new species. Some workers have recognized intraspecific and ontogenetic variation: e. g., Engel & Hummelinck (1936: 38) state that the number of teeth per half-row in Dolabrifera dolabrifera (Rang, 1828) increases with the size of the animal, and Gonor (1961:91) records a similar observation for the tooth rows of Aplysiopsis smithi (Marcus, 1961).

Regression analyses of radular size and numerical variables have been applied only recently to opisthobranchs. Beeman (1963) graphed the number of lateral teeth vs. total body length of *Phyllaplysia taylori* Dall, 1900, and Thompson (1958) graphed the estimated age in months vs. number of rows and size of the lateral teeth of *Adalaria proxima* (Alder & Hancock, 1854); neither calculated the regression lines of his plots, but a visual examination of their graphs indicates that their correlations probably are statistically significant.

The first use of regression analysis formulae to prove statistically that the radular sizes and numerical variations of certain opisthobranch species are ontogenetic differences in size was by Bertsch (1976 a). The method has also been applied by Ferreira (1977) to Triopha maculata MacFarland, 1905, and T. catalinae (Cooper, 1863), and by Bertsch & Meyer (in prep.) to Discodoris heathi MacFarland, 1905, and D. mavis Marcus & Marcus, 1967. These studies have shown that for certain opisthobranch groups, the size of the radula, and the numbers of rows of teeth and teeth per half-row increase with the age (size) of the animal. Bertsch (1976 a) predicts within which opisthobranch taxa these variations will occur, and gives suggestions to the use of statistical analyses.

In this work, regression analyses are used in conjunction with light and scanning electron microscopy and examination of whole animal morphology to elucidate the taxonomic relationships of a large assemblage of species. Such a multidimensional approach bases the choice of taxonomically important characters on significance and reliability. For instance, dependence on color patterns is usu-

ally reliable at the species level for chromodorid nudibranchs, but one must take into account changes in this pattern between juveniles and adults (HAEFELFINGER, 1959; Ros, 1974: plt. 2) and adult variation. Grouping species on the basis of coloration (Rudman, 1973) is useful for comparative purposes, but does not indicate generic relationships. It is necessary to use multiple parameters for taxonomic evaluations, so that the animals are viewed as biological, genetic, and ecological entities subject to natural variation.

In this study, all measurements and calculations were made at least twice to improve their accuracy. The rows of teeth were counted on both halves of the radula, and the larger number was used for the calculations. Several rows of teeth were counted on each radula, to determine the maximum number of teeth per half-row. All counts of number of teeth per half-row indicate the maximum number found in each radula. Variations in the number of teeth per half-row exist within a radula because of tooth growth posteriorly and tooth wear anteriorly (BERTSCH, 1976 a: 119; table 2; fig. 5). Using the maximum number found in the tooth rows eliminates the ontogenetic biases. Length and width maxima were measured on flattened, slide-mounted radulae. The formulae for means, standard deviations, regression analyses, confidence intervals and tests of regression coefficients are presented in SIMPSON, ROE & LEWONTIN (1960: 84, 213-230, 238-241); tables of significance probabilities are in the same book (pp. 422, 426).

Radular Teeth

Definitions of Structural Terms

Descriptions of radulae have included a wide variety of terms with inconsistent usage. To help standardize radular descriptions, Figure 1 illustrates the morphological terms used in this paper for the various parts of a chromodorid radular tooth.

The base (Figure 1, a) of the tooth joins the radular ribbon; the functional, rasping part grows upward as the erect shaft (Figure 1, b). The shaft curves postero-dorsally, and terminates in a point.

Careful discrimination of the different sides of the teeth requires orienting the teeth in the resting stage when the radula is not extended. Along the cephalo-caudal axis of the animal's body, the forward, convex surface of the shaft is anterior. The concave side behind the shaft is posterior (termed "inner margin" by Bloom, 1976). The lateral, left and right, sides of the shaft are more properly

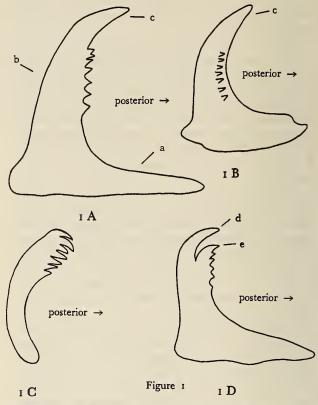


Illustration of structural parts of Chromodoridinae radular teeth

- A. Unicuspid tooth with posterior denticulation; a base; b - erect shaft; c - cusp
- B. Unicuspid tooth with lateral denticulation; c cusp
 - C. Acuspid tooth (after Bertsch, 1976b)
 - D. Bicuspid tooth; d main (or primary) cusp; e - secondary cusp

designated inner and outer faces. The inner face is closest to the rachidian or mid-line of the radula.

Denticles usually occur on the posterior (Figure 1 A) or lateral (Figure 1 B) surfaces of the teeth. When the denticles are significantly smaller than the point on the erect shaft, the point is termed a cusp (Figure 1, c). A unicuspid tooth terminates in one large cusp (Figures 1 A, 1 B), and a bicuspid tooth terminates in 2 cusps larger than the denticles (Figure 1 D). The most distal cusp of a bicuspid tooth is termed the main (or primary) cusp (Figure 1, d), and the more proximal cusp (and also closer to the denticles) is the secondary cusp (Figure 1, e). The shaft of an acuspid tooth (Figure 1 C) termi-

nates in a point smaller than, or of equal size with, the succeeding denticles, and is also called a denticle. Teeth with cusps have a serrate (posterior or lateral) denticulation (Figures 1 A, 1 B, 1 D) and acuspid teeth exhibit pectinate denticulation (Figure 1 C).

TAXONOMIC COVERAGE

Supra-Generic Taxa

GASTROPODA

Subclass Opisthobranchia

Superorder Nudibranchia

HOLOHEPATICA

Doridoidea

CHROMODORIDIDAE

A family of cryptobranch dorid nudibranchs; usually with bright colors and smooth dorsal skin texture (at times the dorsum may have small, low, round tubercles), with lamellate rhinophores and gills surrounding anus. Receptaculum seminis attached to vagina or bursa copulatrix. Radular teeth numerous; erect shaft thicker along anteroposterior axis than laterally; denticles usually present; shaft of tooth may end distally as unicuspid, bicuspid, or acuspid.

Cadlininae

Characters of the family, but usually colored cream or yellow, and dorsal skin surface covered with small, low, round tubercles, or smooth. Rachidian tooth well developed, having a solid erect shaft with pronounced denticulation laterally; lateral teeth unicuspid. Ecologically are predominantly members of temperate, cooler water faunal provinces.

Chromodoridinae

Characters of the family; almost always brightly colored (when seen in laboratory aquaria, intertidally, or at greater depths with artificial lighting). Rachidian tooth not well developed; erect shaft of a small triangular shape, or recurved, thin and narrow; without prominent lateral denticulation. Erect shafts of lateral teeth unicuspid, bicuspid, or acuspid; with lateral or posterior denticles or occasionally smooth.

The familial and subfamilial divisions of the cryptobranch dorid nudibranchs have not been agreed upon consistently in recent literature. Odhner (in Franc, 1968: 866-867) gives full family status to Echinochilidae (with 2 subfamilies, Echinochilinae and Lissodoridinae) and Chromodorididae (Echinochilidae is based on the rejected genus Echinochila Mörch, 1869; the proper name is Cadlinidae; cf. ICZN Opinion 812, 1967). Ros (1975: 320-321) uses Cadlinidae and Glossodorididae. KAY & Young (1969) and Marcus & Marcus (1967) treat Chromodoridinae as a subfamily of Dorididae. The MARcuses (op. cit.) discuss Cadlina Bergh, 1878b, but do not separate the group on a supra-generic level. Schmekel (1972) gives familial status to Chromodorididae and Dorididae. LANCE (in KEEN, 1971: 821-823) recognizes Chromodoridinae and Cadlininae as subfamilies of Chromodorididae (but then erroneously places the Discodoridinae and Inudinae within this same family).

The most natural grouping is to separate Dorididae from Chromodorididae at the family level, and retain Chromodoridinae and Cadlininae. There is a suite of characteristics proper to each family and shared by the respective genera and species:

- a) Body Form and Texture. The Chromodoridinae all have a smooth dorsal surface; some of the Cadlininae show a slightly more rugose texture, with low, rounded tubercles, but members of this group (e. g., Cadlina evelinae Marcus, 1958) have a smooth dorsum. The Dorididae tend to have much larger tubercles, and a rougher texture of the dorsum. This difference is not absolute, but in general is a fairly reliable external separation between the families. It is the least important phylogenetic characteristic because some Chromodorididae show a rougher body texture and because smooth body texture occurs in a number of unrelated dorid forms: e. g., Aphelodoris antillensis Bergh, 1879b, and Dendrodoris krebsii (Mörch, 1863).
- b) Reproductive System. The triaulic cryptobranch dorid reproductive system exhibits little functional and morphological variation (GHISELIN, 1966: 348-349). However, despite this overall homogeneity, the structural arrangement of parts of the female reproductive organs shows 2 patterns, a chromodorid arrangement and a dorid arrangement. These are fairly significant variations; they are not a loss of parts nor a relative difference in size, but

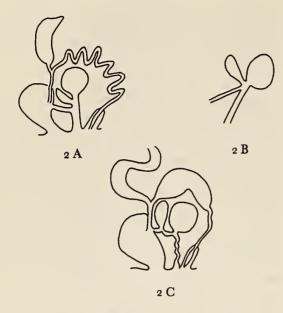


Figure 2

Schematic comparative drawings of Chromodorididae and Dorididae reproductive systems

- A. Chromodorididae reproductive system (after Schmekel, 1972: fig. 50).
- B. Chromodorididae reproductive system, showing (clockwise from the bottom) vagina, insemination duct, receptaculum seminis and bursa copulatrix attached closely.
- C. Dorididae reproductive system (after SCHMEKEL, 1972: fig. 57)

a gestalt configuration. In Chromodorididae (Figure 2 A) the receptaculum seminis is attached to the distal portion of the vagina (near the bursa copulatrix), or to the bursa copulatrix; it is not attached to the central portion of the insemination duct. At times the attachment points of the vagina, receptaculum seminis, and insemination duct are all close together on the bursa copulatrix (Figure 2 B). The typical dorid arrangement (Figure 2 C) has the receptaculum seminis attached near the middle of the insemination duct.

This configuration is uniform throughout the Chromodorididae, and there are only a few exceptions among the other dorids. From tropical west American waters, *Doriopsilla janaina* Marcus & Marcus, 1967, has a chromodorid-type reproductive system (Marcus & Marcus, 1967: 97; fig. 125). It is immediately distinguished from a chromodorid because it is a porostome and it has a rough, highly tubercled dorsum. In 2 Mediterranean species, *Doris verrucosa* Cuvier, 1804 (authorship and date *fide*

SCHMEKEL, 1968) and Doris ocelligera (Bergh, 1881), the reproductive systems' arrangement approaches that of the Chromodorididae. The receptaculum seminis is attached to the insemination duct near the latter's attachment with the vagina (SCHMEKEL, 1968: figs. 2, 4, 8); a dorsum covered with large tubercles and the shape of the radular teeth clearly separate these species from the Chromodorididae. It is of special note, showing that these are rare exceptions to the general rule, that related species in these genera have the typical Dorididae reproductive system arrangement, with the receptaculum seminis clearly attached to the insemination duct: cf. the drawing of Doriopsilla nigromaculata (Cockerell, in Cockerell & Eliot, 1905) by MARCUS & MARCUS (1967: 206; fig. 62C) and of Doris marmorata Risso, 1818, by SCHMEKEL (1968: figs. 6d and 8).

c) Radula. The shape of the lateral teeth is the most characteristic feature of the Chromodorididae. Each tooth (Figure 1) has a thin, knifelike, erect shaft, usually with denticles. By contrast, the teeth of Dorididae (cf. Marcus Marcus, 1967: 81, 83, 86, etc.) are much more hook or sickle shaped, and broader laterally than are those of Chromodorididae. In addition, within the Chromodorididae, subfamily and generic separations are based on major differences of radular morphology.

By using jointly the 3 characteristics of body form and texture, reproductive system, and radula, the members of a genus can be placed reliably within (or excluded from) the Chromodorididae. For example, Bergh (1891) established the Chromodorididae as encompassing 5 genera, including Aphelodoris Bergh, 1879b. Recent usage justifiably excludes Aphelodoris from the Chromodorididae; although the animals have a smooth dorsum, their reproductive system and radular teeth are not chromodorid.

Genera of the Chromodoridinae

ODHNER (in Franc, 1968: 867) included 3 genera in Chromodorididae which are highly problematic. All 3 (Ceratodoris J. E. Gray, in M. E. Gray, 1850; Gruvelia Risbec, 1928, and Otinodoris White, 1948) need further study and adequate descriptions of their radulae and reproductive systems before determining their taxonomic placement. Rosodoris Pruvot-Fol, 1954, was originally placed within the Glossodorididae; it is probably not a Chromodorididae, but its familial relationships are uncertain without additional material. Ceratosoma Adams & Reeve, 1850, is probably a member of the Chromodorididae, but examination of specimens is required to establish its subfamilial status.

The following 8 genera are what I recognize as comprising the Chromodoridinae, with the distinguishing characteristics of their radulae:

Chromodoris Alder & Hancock, 1855 (xvii)

(type genus of the family and subfamily)

Synonym: Felimida Marcus, 1971 (see Thompson, 1972: 398, for additional synonymy).

Type Species: Doris magnifica Quoy & Gaimard, 1832 (= D. quadricolor Rüppell & Leuckart, 1831).

Radular teeth unicuspid, with serrate denticulation; innermost lateral tooth with denticles on both sides of cusp; strongly recurved erect shafts of approximately 2nd through 8th lateral teeth with denticles on lateral face (some species may have denticles on both sides of the cusps of teeth 1-8); erect shafts of teeth lengthen toward the middle of the half-row, with denticles on posterior surface. Outermost lateral teeth become smaller, and retain denticulation.

Chromolaichma Bertsch, gen. nov.

Type Species: Casella sedna Marcus & Marcus, 1967. Also included: Chromodoris dalli Bergh, 1879c; Chromodoris punctilucens Bergh, 1890a; possibly Chromodoris youngbleuthi Kay & Young, 1969.

Radular rows at least 2-3 times greater than maximum number of teeth per half-row; width: length ratio greater than 1:3; small rachidian tooth usually present; radular teeth unicuspid, with lateral serrate denticulation; outermost laterals smooth (with larger radulae, there is a greater number of smooth outer teeth).

Etymology: "Colorful spear-point," derived from $\tau \delta$ $\chi \rho \widehat{\omega} \mu \alpha$ (color) and $\hat{\eta} \alpha i \chi \mu \hat{\eta}$ (the point of a spear), referring to the bright colors of the living animals and the elongate, spear-like radula; the letter "l" inserted for euphony; generic name feminine.

Mexichromis Bertsch, gen. nov.

Type Species: Chromodoris antonii Bertsch, 1976b.
Also included: Chromodoris porterae Cockerell, 1901;
Chromodoris tura Marcus & Marcus, 1967.
Radular teeth acuspid; pectinate denticulation.

Etymology: "Mexican sea-fish," derived from chromis (sea-fish); generic name masculine.

Thorunna Bergh, 1877 (plate 58, figures 30-32)

Synonym: Noumea Risbec (1928: 165).

Type Species: Thorunna furtiva Bergh, 1877.

Radular formula n·1·0·1·n; first innermost lateral tooth with an extremely enlarged base.

Although recent references (e.g., ODHNER in FRANC, 1968: 867; RUSSELL, 1971: 112) cite 1878 as the date of authorship, Bergh published the new names *Thorunna furtiva* in 1877, accompanied by 3 illustrations. Hence the correct date is 1877.

Babaina Odhner, 1968

ODHNER in Franc, 1968: 867 (not Roller, 1972, which = Babakina Roller, 1973).

Type Species: Glossodoris florens Baba, 1949 (pp. 53, 143-144).

Also included: Babaina arbuta (Burn, 1961), comb. nov. (originally Glossodoris), and Babaina daniellae (Kay & Young, 1969), comb. nov. (originally Hypselodoris). Radular teeth have elongate, narrow, erect shafts; bifid (tooth shaft bifurcates distally, but does not have the prominent anterior primary cusp of Hypselodoris); with-

Casella H. & A. Adams, 1854 (p. 57)

out denticulation.

Type Species: Casella gouldii H. & A. Adams, 1854, = Doris atromarginata Cuvier, 1804.

Living animal with a stiff, smooth mantle margin that is lobed.

Radular teeth unicuspid, lateral teeth hook-shaped with denticles on the outer face; rachidian tooth absent. Principal diagnosis of *Casella* rests on the texture of the notum and the notal margin.

Hypselodoris Stimpson, 1855 (pp. 388-389)

Type Species: Goniodoris obscura Stimpson 1855. Radula usually without a median tooth; lateral teeth bicuspid; inner lateral teeth with denticles on outer face; most of the lateral teeth with posterior denticles on the erect shaft below the secondary cusp.

Felimare Marcus & Marcus, 1967 (p. 62)

Type Species: Felimare bayeri Marcus & Marcus, 1967. Radula "with a rachidian plate nearly as high as the neighboring teeth, provided with a smooth cusp." The single species in this currently monotypic genus has bicuspid lateral teeth; the inner lateral teeth are without denticles, but the outer laterals are denticulate on the posterior surface of the erect shaft. A number of Hypselodoris species possess a similar denticulation pattern. Further study of these species in contrast with those that have denticles on all the lateral teeth, may warrant a re-evaluation of the importance of the enlarged rachidian tooth, and a generic separation based on patterns of denticulation.

These major gestalt patterns of the radulae and their teeth separate the Chromodoridinae into 8 genera. Precise feeding studies are needed to elucidate the functioning differences between these radular patterns. Bloom's (1976) work correlated the degree of bending of radular teeth with division of sponge food resources. Functional morphology studies examining broad patterns of Chromodoridinae radular shapes will show additional separation of feeding resource utilization. For instance, studies of feeding specificity should indicate that members of the Chromodoridinae with narrow, long radulae (e. g., Chromolaichma) will utilize a different sponge prey item than those which have a proportionately wider and shorter radula.

Synopsis of Chromodoridinae Species from the Pacific Coast of America

For comparative purposes, these species are all illustrated in Figure 3.

Chromodoris:

Chromodoris baumanni Bertsch, 1970 Chromodoris sp. (to be named in Part II) Chromodoris marislae Bertsch, in Bertsch et al., 1973 Chromodoris mcfarlandi Cockerell, 1901 Chromodoris norrisi Farmer, 1963 Chromodoris sphoni (Marcus, 1971)

Chromolaichma:

Chromolaichma sedna (Marcus & Marcus, 1967) Chromolaichma dalli (Bergh, 1879c) Synonyms: Chromodoris banksi Farmer, 1963 Chromodoris banksi sonora Marcus & Marcus, 1967

Mexichromis:

Mexichromis antonii (Bertsch, 1976b)

Mexichromis porterae (Cockerell, 1901)

Mexichromis tura (Marcus & Marcus, 1967) (species name ending not changed because of uncertain etymology)

Hypselodoris:

Hypselodoris agassizii (Bergh, 1894)
Synonym: Chromodoris aegialia Bergh, 1904
Hypselodoris californiensis (Bergh, 1879c)
Synonyms: Chromodoris glauca Bergh, 1879b
(nomen oblitum)
Chromodoris universitatis Cockerell,

Hypselodoris sp. (to be named in Part IV)
Hypselodoris lapislazuli (Bertsch & Ferreira, 1974)

(Chromodoris juvenca Bergh, 1898, from Chile, is Cadlina juvenca, and hence not a Chromodoridinae.)

Detailed analyses of each species will appear in Parts II, III, and IV.

Because of length considerations, this study² will appear as 4 separate articles in this journal.

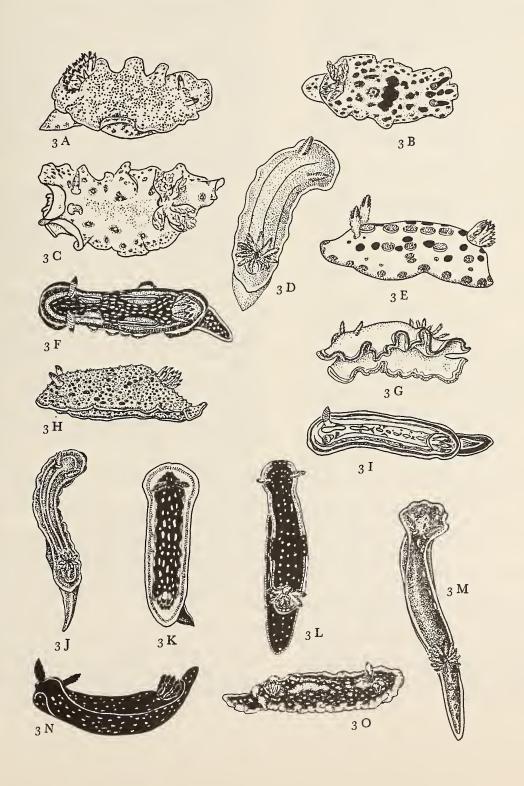
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Figure 3

Drawings of living Chromodoridinae from the American Pacific coast

- A. Chromodoris baumanni (after MARCUS & MARCUS, 1967: 172)
- B. Chromodoris sp. (after color transparencies by Alex Kerstitch)
- C. Chromodoris marislae (after Bertsch et. al., 1973: 294)
- D. Chromodoris mcfarlandi (after MacFarland, 1966: plt. 22)
- E. Chromodoris norrisi (after MARCUS & MARCUS, 1967: 171)
- F. Chromodoris sphoni (after MARCUS, 1971: 356)
- G. Chromolaichma sedna (after MARCUS & MARCUS, 1967: 179)
- H. Chromolaichma dalli (after Marcus & Marcus, 1967: 174)
- I. Mexichromis antonii (after Bertsch, 1976b: fig. 1)
- J. Mexichromis porterae (after MacFarland, 1966: plt. 24)
- K. Mexichromis tura (after Marcus & Marcus, 1967: 52)
- L. Hypselodoris agassizii (after Marcus & Marcus, 1967: 177, fig. 31)
- M. Hypselodoris californiensis (after MacFarland, 1966: plt. 24)
- N. Hypselodoris sp. (after Marcus & Marcus, 1967: 177, fig. 30)
- O. Hypselodoris lapislazuli (after Bertsch & Ferreira, 1974: fig. 1)

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